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Which features at home make a plant prone to become invasive?

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Abstract

Determining the factors that pre-adapt plant species to successfully establish and spread outside of their native ranges constitutes a powerful approach with great potential for management. While this source-area approach accounts for the bias associated with species' regions of origin, it has been only implemented in pools of species known to be established elsewhere. We argue that, in regions with well-known introduction histories, such as the Mediterranean Biome, the consideration of co-dominant non-introduced species as a control group allows a better understanding of the invasion process. For this purpose, we used occurrence data from GBIF and trait data from previous studies to find predictors of establishment and invasion. We compare the frequency, climatic niche and functional traits of 149 co-dominant plant species in their native region in southern Spain, considering whether they have colonised other Mediterranean-climate regions or not and their level of invasion. We found that large native ranges and diverse climatic niches were the best predictors of species establishment abroad. Moreover, coloniser species had longer bloom periods, higher growth rates and greater resource acquisition, whereas coloniser species becoming invasive had also greater reproductive height and nitrogen use efficiency. This framework has the potential to improve prediction models and management practices to prevent the harmful impacts from species in invaded communities.

Keywords

Climatic niche, exotic plants, functional traits, Mediterranean-climate, source-area approach

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Introduction

Exotic plant species pose an increasing threat to native species and ecosystems conservation (Vilà et al. 2011; Bradley et al. 2019). Identifying predictors of invasion success constitutes a fundamental aim in invasion biology in order to support prevention measures and risk assessments (Pyšek et al. 2020). Key factors that drive successful invasion are high propagule pressure (Cassey et al. 2018) and having competitive traits or general-purpose phenotypes that confer ecological versatility and, therefore, high invasiveness (Drenovsky et al. 2012; Casado et al. 2018). Invasiveness also depends on the interaction with ecological and evolutionary processes occurring in the introduced range (Van Kleunen et al. 2010b); therefore, its determinants are context dependent (Novoa et al. 2020), which emphasises the necessity to identify variables that facilitate invasion under specific environmental constraints.

Most studies interested in identifying factors promoting invasion success frequently focus on understanding the mismatch in functional trait performance between exotic species and their native competitors in the recipient communities (e.g. de la Riva et al. 2019; Galán Díaz et al. 2021a). An alternative approach is to compare functional strategies of species from the same source or geographic region (i.e. source-area approach) to identify whether species' occurrence, traits and climatic niche in the native range allow us to predict their establishment and spread when introduced in other regions. This approach accounts for the bias associated with species region of origin and, potentially, allows us to focus on the role of traits alone (Martín-Forés et al. 2023). In this regard, it has been found that the climatic tolerance and ecological versatility of species in their native range are positively correlated with their capacity to establish and spread in other regions (Pyšek et al. 2009, 2015; Casado et al. 2018). This is probably associated with the display of certain trait attributes (Pyšek and Richardson 2007; Pyšek et al. 2009, 2015) and the fact that many exotic species are not only frequent and abundant in their invaded ranges, but also dominate in the communities of their native range (Firn et al. 2011; Galán Díaz et al. 2021b). Yet, most studies following the source-area approach have only looked at species known to be established in other regions, disregarding the role of co-dominant non-colonisers. We argue that, in regions with well-known introduction histories, the consideration of co-dominant non-introduced species as a control group allow us to broaden our understanding of the predictors of invasion success.

Studies following the source-area approach have mainly explored the importance of life history traits as predictors of invasiveness (Pyšek et al. 2009; Arianoutsou et al. 2013; Casado et al. 2018), whereas the role of functional traits in species native ranges has been frequently overlooked (but see Schlaepfer et al. (2010); Pyšek et al. (2015)). Moreover, the combined consideration of above- and below-ground plant functional traits remains little explored in invasion studies (Fridley et al. 2022). Plant traits might be useful to predict invasion success because, under specific environmental constraints, traits that confer dominance in the native range might be the same that facilitate establishment and spread in the introduced range (Thompson et al. 1995). In this regard, it has been shown that exotic species in Mediterranean regions can be functionally different to other species in their native communities (Galán Díaz et al. 2023)

and display phenotypic variation when compared with communities in the introduced range (Martín-Forés et al. 2017, 2018). This might suggest that invasive species could already have intrinsic attributes to establish and thrive in communities with similar abiotic constraints rather than only benefitting from extrinsic ecological and genetic factors (Schlaepfer et al. 2010; Colautti et al. 2014). Therefore, it is important to leverage the performance of plant functional traits within the native range as predictors of the establishment and future stage of the invasion of species in the introduced range. In addition, it is necessary to include measures of phylogenetic relatedness as shared evolutionary histories of species might lead to statistical non-independence of data (Felsenstein 1985; Schlaepfer et al. 2010; Vilà et al. 2015).

Spain is home to many herbaceous species that are naturalised in other Mediterranean-climate regions of the world (Casado et al. 2018). The origin of these introductions can be tracked down to the arrival of the first Europeans settlers into these territories where species were introduced deliberately (i.e. crops, ornamental plants) or accidentally (i.e. weeds introduced with livestock, fodder, wool or cereals) (Barry et al. 2006; Martín-Forés 2017). These species (henceforth coloniser species) co-existed long-term with anthropogenic activities in their native range (Schlaepfer et al. 2010; MacDougall et al. 2018) and benefitted from an initial high propagule pressure. These coloniser species brought novel traits into the recipient communities, such as annual life cycles and efficient resource-use strategies, highly beneficial in a context of farming, intense herbivory, long drought periods and high soil disturbance (Seabloom et al. 2003; Funk and Vitousek 2007; HilleRisLambers et al. 2010; Molinari and D'Antonio 2014). Therefore, Spain communities constitute good candidates to apply the source-area approach.

Here, we compare the occurrence (i.e. frequency), climatic niche and functional traits of co-dominant plant species in their native region in southern Spain considering whether they have colonised other Mediterranean-climate regions or not. Our hypotheses are that: (1) Colonisers are more frequent and show greater climatic tolerances than co-occurring non-coloniser natives. This would reflect the importance of propagule pressure (high association with humans in the native range) and having great ecological versatility; (2) Colonisers are functionally different from non-coloniser species and show traits related to higher resource-acquisition rates and greater competitive ability. This would reflect that coloniser species benefit from niche opportunities or competitive advantages, even in Mediterranean-climate regions where the harsh environmental conditions frequently lead to functional convergence (Galán Díaz et al. 2021b, 2023); (3) Naturalised and invasive coloniser species are functionally distinct in their native range, i.e. certain plant attributes are related to the stage of invasion in other Mediterranean-climate regions.

Material and methods

Grassland surveys

We used trait data from co-dominant grassland species in southern Spain (Andalucía) compiled by Galán Díaz et al. (2022) which is available from Dryad (Galán Díaz et

al. 2022). Dominant species were defined as those whose cumulative cover made up at least 90% of the total community cover (Garnier et al. 2004). We selected as a source species pool all species native to Spain (149 species in total) which were classified as coloniser (98 species) or non-coloniser (51 species), depending on whether they are known to be introduced in other Mediterranean-climate regions of the world or not. We further classified coloniser species according to their stage of invasion or performance in other Mediterranean-climate regions into naturalised (56) and invasive (42) (Arianoutsou et al. 2013; Calflora 2014; Henderson 2020; Pagad et al. 2022). Naturalised colonisers are those species that have established at least in another Mediterranean-climate region; whereas, invasive refers to naturalised species that reproduce and spread fast at least in another Mediterranean-climate region (Richardson et al. 2000; Blackburn et al. 2011). The list of species included in this study can be found in Suppl. material 1: appendix S1.

Occurrence and climate data

Occurrence data of the target species in southern Spain were downloaded via the Global Biodiversity Information Facility (GBIF) using the "rgbif" package (Chamberlain et al. 2022). Although the native range of some species extended beyond this area, we focused on the distribution patterns within the species' native ranges where traits were measured (i.e. autonomous community of Andalusia) because intraspecific variation in species traits can be high across species distribution ranges (Umaña and Swenson 2019). To avoid artefacts related to collection bias and spatial clustering (Larridon et al. 2021), we filtered one observation per species and cell from a raster with a resolution of 30 seconds (0.86 km^2 at the Equator) which represents species frequency or number of grid cells occupied by the species. For the filtered observations, climate data were obtained from WorldClim at a resolution of 30 seconds (Fick and Hijmans 2017). We used the variables Annual Mean Temperature, Maximum Temperature of Warmest Month, Temperature Annual Range, Annual Precipitation, Precipitation of Driest Month and Precipitation Seasonality which represent average, extreme and seasonal indexes of temperature and precipitation.

Functional traits measurements

We considered eight functional traits that reflect orthogonal axes of plant function related to plant investment in above- and belowground vegetative and reproductive structures and community assembly processes (Table 1; Garnier et al. 2016; Hulme and Bernard-verdier 2018). Traits were measured in 149 species (301 combinations of species × site). A detailed description of the methodology followed to measure each trait can be found in Galán Díaz et al. (2022). In addition, we retrieved another 13 traits from literature related to life and growth form, reproduction strategies, pollination vectors and dispersal vectors (Table 1; the list of references can be found in Suppl. material 1: appendix S2).

Table 1. Traits considered in this study. Traits marked with an asterisk were retrieved from literature (the list of references can be found in Suppl. material 1: appendix S2).

	Trait	Abb.	Units	Significance
	Growth form *			Bulbous/Erect/Graminoid/Prostrate/Rosette
	Life form *			Therophyte/Geophyte//Hemicryptohpyte/Chamephyte
Leaf	Specific leaf area	SLA	cm^2/g	Resource acquisition rate and conservation, photosynthetic rate, relative growth rate
	Leaf dry matter content	LDMC	mg/g	Leaf tissue density, resistance to physical hazards, stress tolerance
	Ratio C:N	CN		Resource allocation
	Isotopic carbon fraction	$\delta^{13}C$	‰	Integrated water use efficiency
Root	Specific root length	SRL	cm/mg	Resource acquisition rate and conservation, relative growth rate
	Root dry matter content	RDMC	mg/g	Root tissue density, resistance to physical hazards, drought resistance
	Root diameter	RD	mm	Mycorrhizal association
Reproduction	Reproductive height		cm	Dispersal capacity
	Seed mass *		g	Seedling survival and establishment
	Onset of flowering *	OFL	months	Reproductive success
	Length of bloom *	LB	months	Reproductive success
	Self-compatibility *		1/0	
	Pollination mechanism *			Insects/Wind/Selfed
	Dispersal vector *	Agochory	1/0	Humans
		Autochory	1/0	Self-dispersed
		Anemochory	1/0	Wind
		Hydrochory	1/0	Water
		Zoochory	1/0	Animals
	Number of dispersal vectors *	numb_disp	1–5	

Statistical analyses

First, to estimate species' climatic niches, we performed a Principal Component Analysis (PCA) with the six climatic variables and used the scores of the observations along the first three Principal Components (PCs) to calculate two indexes (Suppl. material 1: appendix S3): (i) climatic niche richness, calculated as the smallest convex hull that encloses all observations of a given species; and (ii) climatic niche diversity, calculated as the mean pairwise distance amongst observations of a given species. These indexes represent two independent facets of species climatic niches. While climatic richness represents the dispersion or range of species climatic niches, climatic diversity indicates how the observations are distributed within the convex hull. The mean pairwise distance is less sensitive to outliers and is better correlated to the number of different habitats occupied by the species in their native range, a known predictor of invasiveness (Pyšek et al. 2015). We used linear models to compare whether the species frequency and climatic niches differ between non-coloniser, naturalised and invasive species.

Second, we compared trait differences between non-coloniser and coloniser species and differences between naturalised and invasive species within non-colonisers. For

continuous traits, we used the median value per species. Reproductive height and seed mass were log-transformed prior to analyses. We ran linear models to test for differences in continuous traits and chi-squared tests for categorical data. We ran Wilcoxon rank-sum and Kruskal-Wallis tests for onset of flowering, length of the bloom period and number of dispersal mechanisms. To test for the effect of phylogenetic non-independence amongst species (i.e. whether the observed patterns reflect contrasting evolutionary histories), we ran a phylogenetic ANOVA using the aov.phylo function implemented in the "geiger" package (Pennell et al. 2014). For this, we used an existing megaphylogeny to obtain a phylogenetic inference of our study species (Qian and Jin 2016). Species which were missing in the original tree were substituted by congeneric species (de la Riva et al. 2019). The phylogenetic inference is available in Suppl. material 1: appendix S4.

Third, we ran a supervised classification algorithm (random forest) to leverage the relative importance of species occurrence (i.e. frequency), climatic niches and traits as predictors of invasiveness. We removed qualitative traits with missing data and imputed continuous traits using the rfImpute function included in the "randomForest" package. We also included family as a predictor because of the importance of phylogenetic relationships inferred from the phylogenetic ANOVA.

All statistical analyses were performed in R version 4.2.2. To ensure the results of this study are fully reproducible, codes are available from GitHub (https://github.com/galanzse/colonizersathome) and data from the Dryad Digital Repository (Galán Díaz et al. 2022).

Results

Coloniser species were more frequent than non-coloniser species in their shared native range in southern Spain and had greater climatic niche richness and diversity (Fig. 1). When considering the stage of invasion in other Mediterranean-climate regions, naturalised species were more frequent than non-coloniser species; both coloniser groups (i.e. naturalised and invasive species) had similar climatic richness and greater climatic richness than non-colonisers; and invasive species had greater climatic diversity than non-coloniser and naturalised species (Fig. 1).

We found significant functional differences between non-coloniser and coloniser species for four traits: specific leaf area (SLA), specific root length (SRL), length of bloom period and number of propagule dispersal vectors (Fig. 2 and Table 2). Coloniser species had on average 17.68% greater SLA and 15.23% greater SRL than non-coloniser species. The bloom period of coloniser species was one month longer than non-coloniser species. Coloniser species showed more propagule dispersal vectors than non-colonisers.

We found significant differences between groups when considering the stage of invasion of colonisers in other Mediterranean-climate regions (Fig. 3). Naturalised colonisers had on average 23.20% greater SLA than non-colonisers and their bloom periods were one month longer. Invasive colonisers were 11.03% taller and had 20.78%

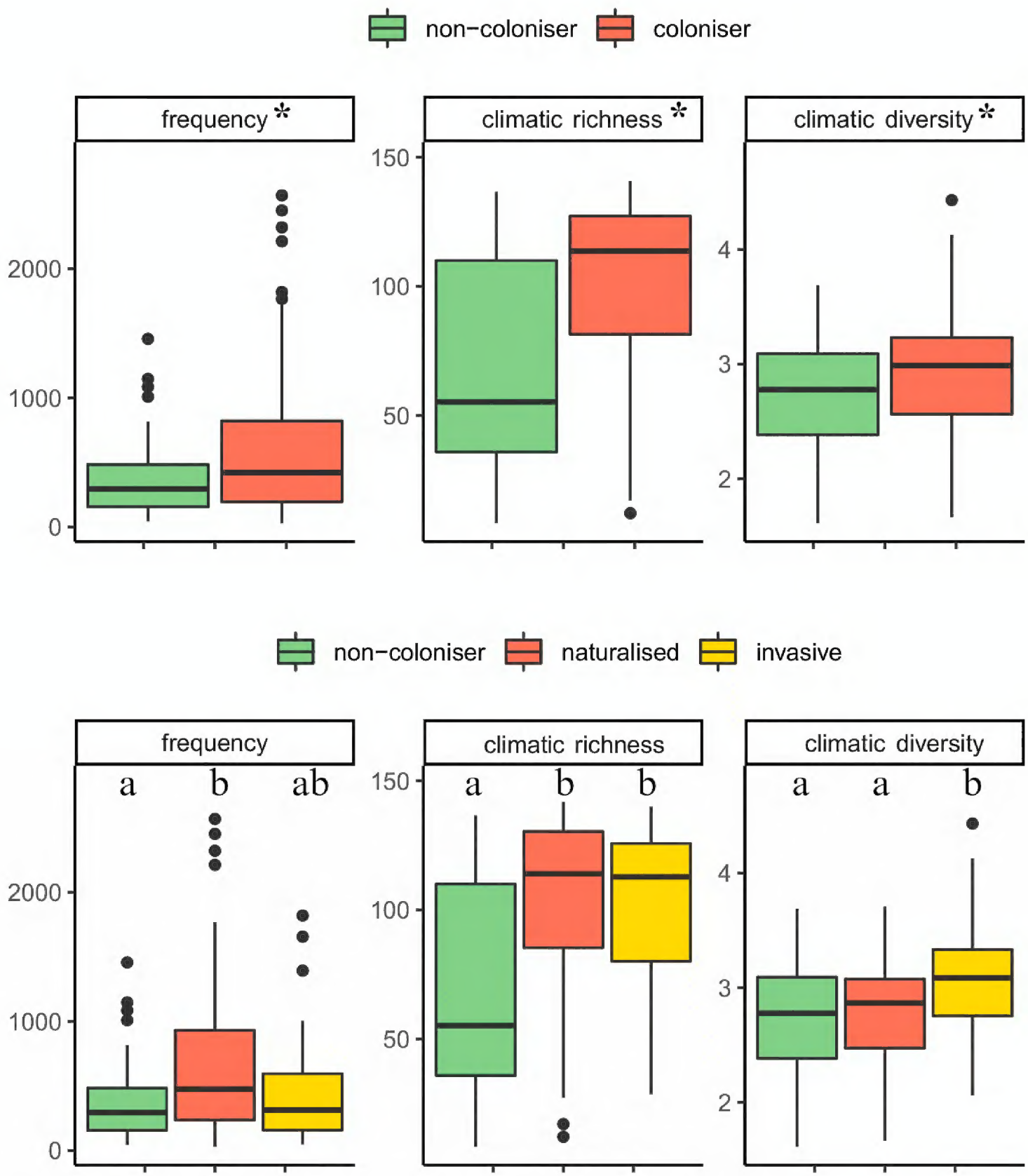

Figure 1. Species frequency (i.e. number of cells occupied in the native region), climatic niche richness (i.e. smallest convex hull that encloses the observations) and climatic niche diversity (i.e. mean pairwise distance amongst occurrences) of non-coloniser and coloniser species, also considering the stage of invasion of coloniser species (i.e. naturalised or invasive) in other Mediterranean-climate regions.

greater C:N than naturalised colonisers. Both naturalised and invasive coloniser species showed more propagule dispersal vectors than non-colonisers.

The phylogenetic ANOVAs revealed that evolutionary relatedness does not necessarily determine trait differences between non-coloniser and coloniser species, but plays a major role when considering the stage of invasion of colonisers. Functional

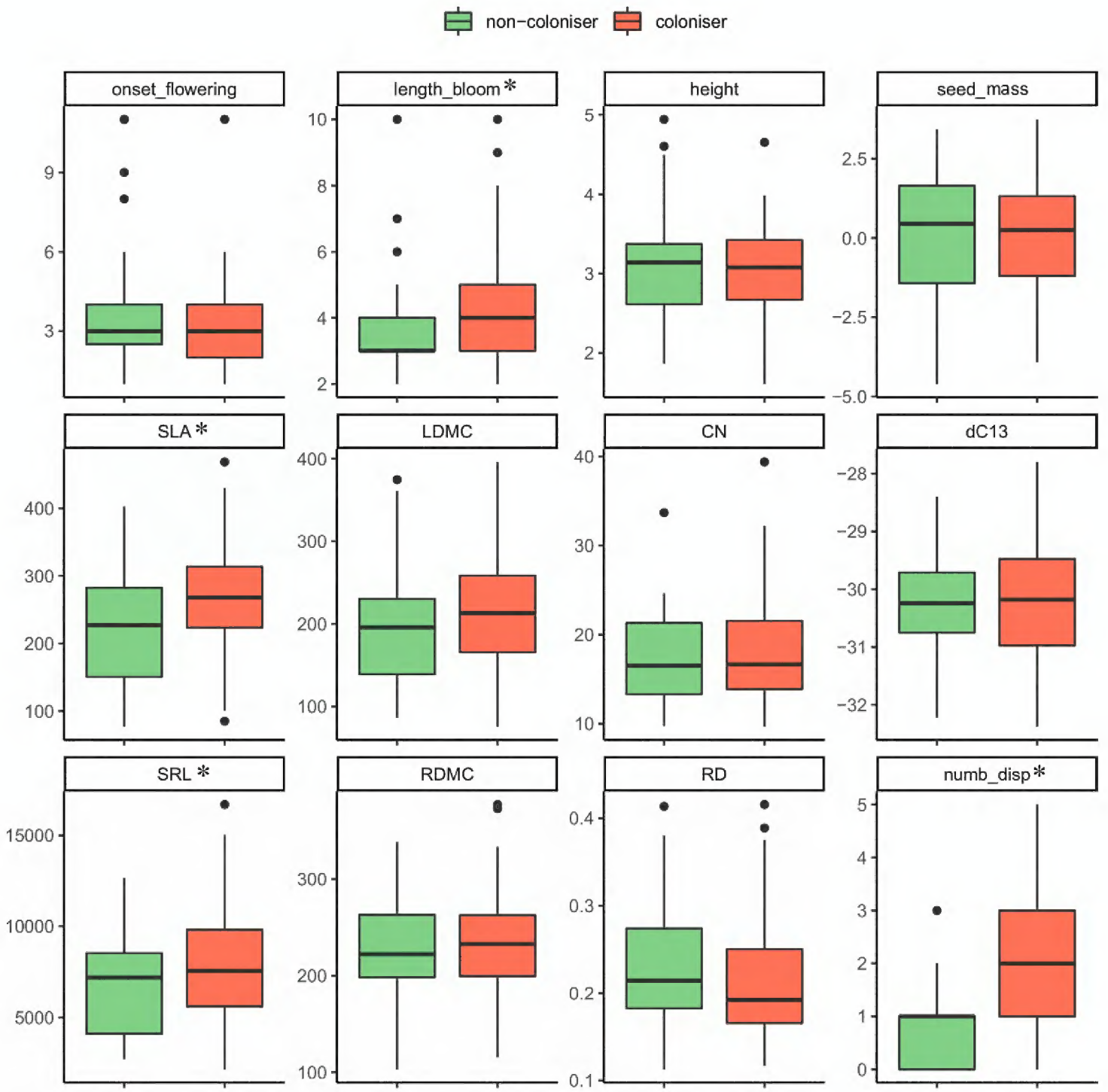

Figure 2. Functional differences between non-coloniser and coloniser species. * p-value < 0.05.

differences between non-coloniser, naturalised and invasive species may reflect phylogenetic non-independence amongst groups, mostly due to the large proportion of invasive grasses (Suppl. material 1: appendix S5).

Non-coloniser and coloniser species differed in many qualitative traits (Table 2). Naturalised coloniser were more frequently therophytes, whereas invasive colonisers were more frequently grasses and, therefore, pollinated by wind more than the other groups. More than fifty percent (51.02%) of coloniser species were reported to be self-compatible in contrast to 15.68% of non-coloniser species. Overall, coloniser species presented more dispersal vectors than non-colonisers.

The accuracy of the random forest model was 73.53% when predicting coloniser/non-coloniser species (Table 3). The most important variables that contributed to this model were richness of the climatic niche, dispersal vectors, agochory, family and zoo-

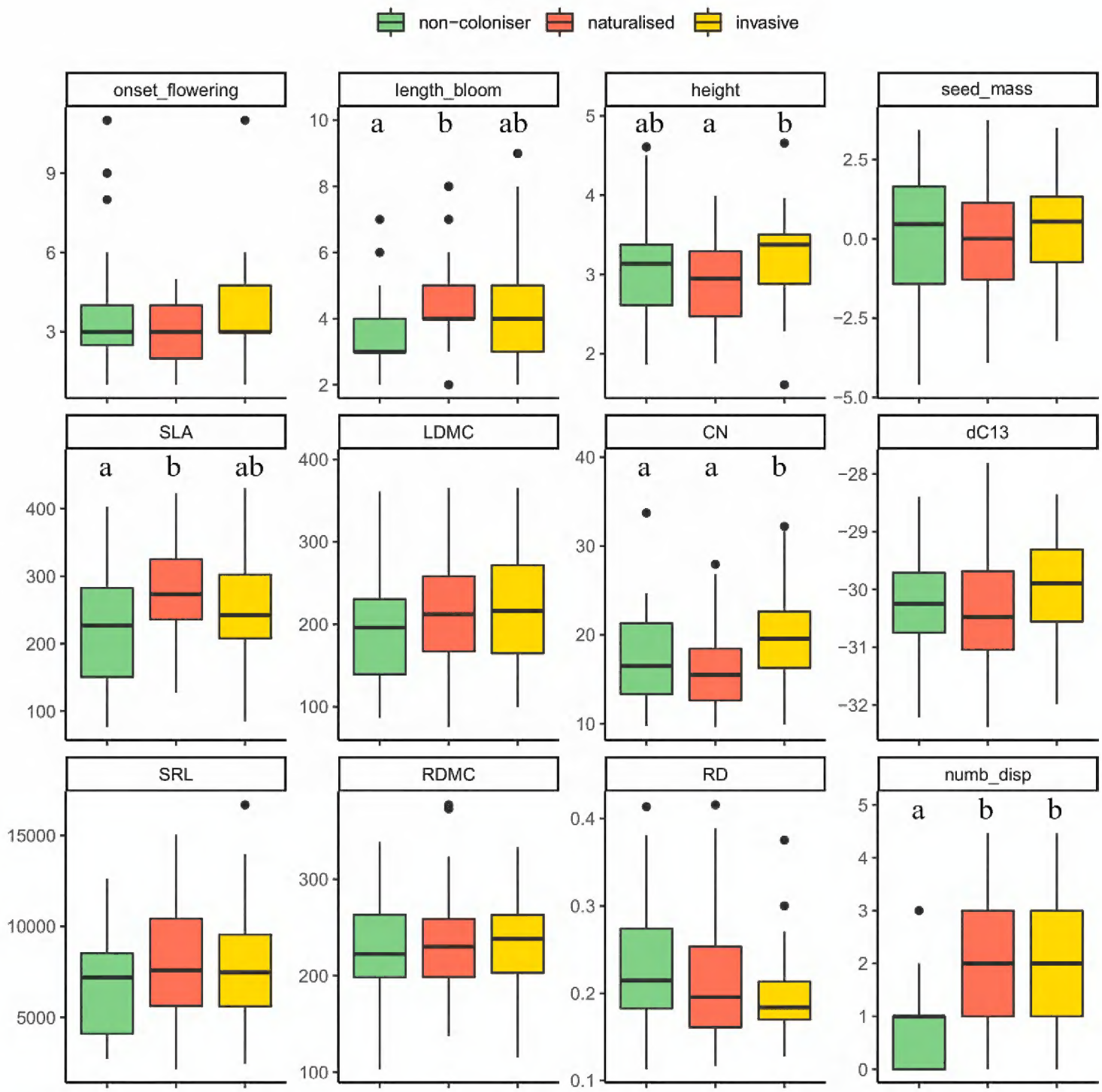

Figure 3. Functional differences between non-coloniser, naturalised and invasive species. Letters denote statistical differences in post-hoc comparison (p-value < 0.05).

chory (Fig. 4). The inclusion of the stage of invasion decreased the accuracy of the model to 58.82%. The most important variables that contributed to the model specifying the stage of invasion were richness of the climatic niche, dispersal vectors and family.

Discussion

Discerning general invasion syndromes across ecosystems can facilitate the identification of species with greater risks of establishment and support management actions at different stages of the invasion process (Novoa et al. 2020). In this study, we looked at the occurrence, climatic niches and traits of a pool of co-dominant grassland plant

Table 2. Contingency table of qualitative traits of non-coloniser and coloniser species. Coloniser species are separated considering their level of invasion in other Mediterranean-climate regions. * p-value < 0.05.

	trait	non-coloniser (n = 51)	coloniser (n = 98) naturalised (n = 56)	coloniser (n = 98) invasive (n = 42)
Life form	therophyte	32	51	28*
	geophyte	2	1	0
	hemicryptophyte	10	4	13
	chamephyte	3	0	1
Growth form	bulbous	3	1	0
	erect	26	28	17*
	graminoid	4	6	17*
	prostrate	13	18	4*
	rosette	2	3	4
Pollination	insects	32	38	18*
	wind	6	9	21*
	self-compatible	8	33	17*
Dispersion	agochory	2	22	23*
	anemochory	12	19	23*
	autochory	4	24	6*
	hydrochory	1	12	11*
	zoochory	13	36	28*

Table 3. Confusion matrices of random forest models. Rows indicate the actual (true) values for each category and columns indicate predicted values. The classification error corresponds to the proportion of wrongly classified cases, i.e. for a given category, the classification equals to the number false negative predictions divided by the total number of actual cases.

		predicted			
	Model 1	**coloniser**	**non-coloniser**		**classification error**
actual	coloniser	79	16		0.17
	non-coloniser	20	21		0.49
	Model 2	invasive	naturalised	non-coloniser	
	invasive	18	13	10	0.56
	naturalised	11	36	7	0.33
	non-coloniser	6	9	26	0.37

species in their native range in southern Spain to explore its utility as predictors of invasiveness in other Mediterranean-climate regions of the world.

We found that coloniser species are more widespread (i.e. frequent) in their native region than co-dominant non-coloniser species. This result matches the Casado et al. (2018) positive relationship between the degree of occurrence of herbaceous species in their native range in the Iberian Peninsula and their capacity to successfully occupy other Mediterranean-climate regions. This evidence also adds to previous studies that reported high abundances of coloniser species in their native Mediterranean communities (Firn et al. 2011; Galán Díaz et al. 2021b). This trend, therefore, suggests that the more frequent and dominant species are in their native region, the greater the

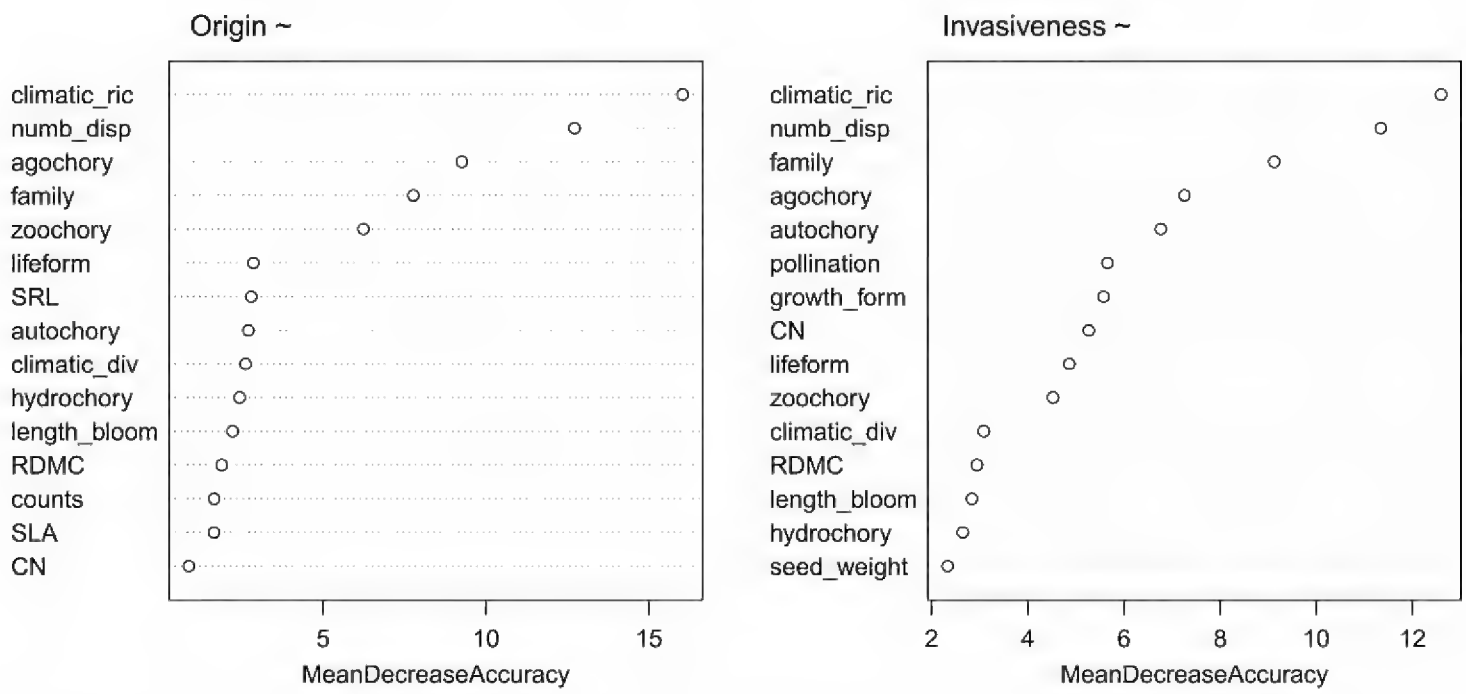

Figure 4. Variable importance plot of random forest classification models. Origin indicates whether the species are introduced in other Mediterranean-climate regions of the world (i.e. non-coloniser and coloniser). Invasiveness refers to species' stage of invasion in other Mediterranean-climate regions (i.e. non-coloniser, naturalised and invasive).

probability of coming into contact with humans and the higher the propagule pressure, ultimately facilitating their establishment (Cassey et al. 2018). We also found a positive relationship between the frequencies of coloniser species in their native ranges and their climatic niche richness and diversity, i.e. coloniser species occupy a large proportion of climatically different areas in their native range reflecting their ecological versatility. When considering invasion status, naturalised colonisers were more frequent than non-coloniser species and, whereas we did not find evidence supporting a greater frequency of invasive colonisers than non-colonisers, invasive colonisers showed the greatest diversity in terms of their climatic niche. Similarly, Pyšek et al. (2009, 2015) found that the number of habitats that a species occupies in its native range is positively correlated to the number of regions where it has successfully established abroad. As naturalised and invasive species showed similar climatic niches in terms of richness, this result reflects that colonisers' capacity to fully occupy their climatic and ecological niches in the native range is a good predictor of their capacity to overcome the dispersal and environmental barriers abroad and become invasive (Blackburn et al. 2011).

There were functional differences between non-coloniser and coloniser species. Overall, coloniser species achieve a combination of traits that facilitate rapid growth, regeneration and spread compared to non-coloniser species. That is, colonisers species displayed greater SLA and SRL, which indicates high resource-use efficiency and relative growth-rates (i.e. high C gain and leaf production when resources are abundant; Funk et al. (2017); Fridley et al. (2022)) and higher rates of N uptake (Jo et al. 2015, 2017). Similar trends have been reported across communities of the Mediterranean Biome (Galán Díaz et al. 2021a) and globally (Ordonez and Olff 2013; Fridley et al. 2022). Our findings also indicated that leaf traits of colonisers appear to be coordinated

with root traits, which suggests that synchronisation amongst organs as part of a whole-plant resource uptake strategy is common in Mediterranean plants (de la Riva et al. 2016, 2021). Moreover, we found that coloniser species had longer length bloom periods, which indicates a greater investment in reproductive structures. Hence, coloniser species may benefit from reduced competition via exploiting different temporal niches (Godoy et al. 2009), thereby increasing the chances of producing viable propagules by potentially covering broader seasonal ranges and climatic conditions (Grubb 1977). Coloniser species showed more propagule dispersal vectors (both naturalised and invasive species) than non-coloniser ones. This variety of dispersal vectors provides an advantage when they come into contact with humans in the native region and spread across other regions after establishment (Pyšek and Richardson 2007; Blackburn et al. 2011). Both naturalised and invasive colonisers showed a greater proportion of self-compatible species than non-colonisers. It has been argued that self-compatibility could facilitate the establishment of exotic species but, hinder species of becoming invasive (Pyšek and Richardson 2007). Yet, multiple introductions are frequent and within-population genetic diversity of introduced populations has been found to be comparable to native populations (Bossdorf et al. 2005); therefore, the possibility of self-fertilisation could be an advantage at every stage of the invasion process. This collated evidence suggests that coloniser species could benefit from niche opportunities or competitive advantages in their native region (Galán Díaz et al. 2021b, 2023). These functional differences could present an advantage in anthropogenic habitats globally if they reflect adaptation to agricultural and managed habitats (MacDougall et al. 2018).

As we pointed out, maximising resource uptake and high relative growth rates has been observed as a successful strategy for coloniser species. However, when considering invasion status, the patterns were more nuanced: we did not find significant differences in SRL associated with invasion status and the species displaying the highest SLA and longer bloom periods were naturalised instead of invasive colonisers. Invasive species, in turn, displayed higher values of reproductive height, which is closely correlated to plant stature in grassland species and C:N concentration. Therefore, different traits might be relevant along different stages of the invasion process (Pyšek et al. 2015; Milanović et al. 2020). On the one hand, higher rates of growth and resource acquisition might facilitate plant survival and establishment in seasonal climates with dry seasons such as the Mediterranean (Funk et al. 2016; Galán Díaz et al. 2021a). Additionally, the longer length bloom periods of naturalised species compared to non-colonisers, which were also frequently pollinated by insects, suggests that the potential to participate in native plant–pollinator networks might result in being beneficial (Parra-Tabla and Arceo-Gómez 2021). On the other hand, our results reflect the importance of greater dispersal distance and above-ground competitive hierarchy and competition for light to overcome the dispersal barrier and become invasive (Schlaepfer et al. 2010; Bernard-Verdier et al. 2012). Reproductive height constitutes a well-known driver of invasiveness (Van Kleunen et al. 2010a; Gallagher et al. 2015; Divíšek et al. 2018) and it has been shown that invasive grasses transform grassland native communities by filtering tall native species that can compete for light (Molinari and D'Antonio 2014).

Higher C:N ratio indicates high nitrogen use efficiency in nitrogen-limited communities (Zhang et al. 2020).

The phylogenetic regressions suggest that some observed differences across stages of invasion may be masked by evolutionary relatedness amongst groups: naturalised species were more frequently forbs, whereas invasive colonisers were more frequently grasses. For instance, invasive species not displaying significantly greater SLA than non-colonisers, but showing greater C:N, might reflect greater carbon allocation to leaves in grasses than in forbs (Duffin et al. 2019). In addition, naturalised species were more frequently pollinated by insects, whereas invasive colonisers were more frequently pollinated by wind. The little dependency of invasive species for insect pollination might increase the chances of producing viable propagules. This suggests that trait comparisons expecting competition within the LHS strategy scheme might not be useful to completely understand community assembly processes along different stages of the introduction process (Westoby 1998) and that niche complementarity in terms of life forms, pollination and dispersal vectors are key aspects to consider.

The two most important predictors of the random forest models were climatic richness and number of dispersal vectors. Family was an important variable reflecting the importance of considering evolutionary relatedness in biological invasions to account for unmeasured trait diversity and to correctly interpret the observed differences (Felsenstein 1985; Schlaepfer et al. 2010; Vilà et al. 2015). Agochory (i.e. accidental spread of plants by humans) also contributed to the overall accuracy of the models, suggesting that species with propagules suspected of being dispersed by (and associated with) humans are those with higher probabilities of establishing abroad (MacDougall et al. 2018). However, the first model did not allow us to differentiate non-coloniser species with the capacity to establish in other regions or, conversely, this might suggest that some non-coloniser species could have the climatic tolerance and traits to do so. The second model yielded very low overall performance because of the great overlap between naturalised and invasive colonisers in the distribution of the predictor variables. It is worth noting that functional traits constituted poor predictors of species establishment and invasiveness compared to climatic or ecological tolerance indexes. Therefore, our findings support that, whereas functional traits have the potential to capture community assembly processes (Galán Díaz et al. 2023) or intraregional distribution patterns (Pyšek et al. 2015), traits alone might not directly relate to the stage of invasion in most habitats (Fridley et al. 2022).

Conclusions

We have shown that coloniser species are already pre-adapted to broader climatic niche conditions in their native range, which predisposes them to occupy greater diverse conditions once they are introduced in a new area. In a similar manner, certain traits, especially indicating aided dispersal, high relative growth rate and resource efficiency, are related to successful colonisation; whereas, invasion processes in grasslands are more

associated with plants displaying higher reproductive height and nitrogen use efficiency. The source-area approach can be especially useful when comparing regions with shared histories of colonisation and trade where plant introduction histories have been mostly unidirectional as is the case of the Mediterranean Biome. The knowledge derived from such studies may allow us to improve prediction models, identifying key species to monitor; this could, therefore, prevent potential harmful impacts from coloniser species in invaded communities and reduce the investment necessary to target eradication measures.

Author contributions

JGD: Conceptualisation, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review and editing. EGR: Methodology, Supervision, Writing - review and editing. IMF: Investigation, Writing - review and editing. MV: Conceptualisation, Supervision, Funding acquisition, Writing - review and editing.

Data availability statement

The data and codes used in this study are archived in Dryad and Github.

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Supplementary material 1

Species list, references accessed during bibliographic research, phylogenetic inference used in the analyses, PCA of climatic variables, and results of linear regressions

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Data type: species, references, phylogenetic, models

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